Copepod taxonomy: Discovery vs. recognition

David M. Damkaer

21318-195th Ave. SE, Monroe, Washington 98272-9481, U.S.A.

Abstract.—A table of copepod orders, families, and type genera, with authors and dates, revealed a general marked delay between the discovery of a genus and the establishment of higher taxa based on that genus. The average time from genus definition to order definition was 51 yr. For families, this delay was 31 yr, with a range of 0 to 159 yr. Excluding the 54 families defined simultaneously with the discovery of their type genus, the average delay was 42 yr. The future trajectory of accumulating family definitions is discussed. The present dynamics of copepod taxonomy may require additional decades before a falling off of new orders and families can be predicted.

A recently published copepod classification (Bowman & Abele 1982), in contrast to many such summaries, indicated authors and dates for taxa down to family. Since that publication, other authors have made additions or alterations to this classification (Fosshagen & Iliffe 1985, 1989; Ho 1990, 1991; Kim 1991, Grygier 1994). A revised classification of the current 10 copepod orders and 205 families is given in Table 1; changes from the table of Bowman & Abele are indicated. It became of interest to plot the establishment of the listed families by decade (Fig. 1), as a representation of the historical awareness of copepods as a large, distinct group of Crustacea. What is apparent is a steady increase in defined families over 160 yr, with at least four periods of exceptionally rapid progress. These periods can be attributed mostly to James Dwight Dana (1840s and 1850s), to Wilhelm Giesbrecht (1890s), to Georg Ossian Sars (1900s and 1910s), and to several investigators since 1950. Besides an obvious expression of personal energy, the association of those periods with individuals reflects in part an ability to sample in or obtain material from a wide variety of new habitats. There is also a necessary time-lag, since in any era there had to be a reasonable background of described species against which

the higher taxa could be discerned. [Note that an investigator could have defined nearly any and all of these higher taxa from literature, without once looking at a specimen—fortunately, this was not the case.]

A second relationship (Fig. 1) shows the establishment of the highest taxa within Copepoda, namely the eight orders into which the subclass was divided, as given by Bowman & Abele (1982), and two orders added in the subsequent decade (see Ho 1990). Again, this indicated a steady increase over the same long time. But was the establishment of these 10 orders, and their contained families as well, indicative of newly discovered fundamental copepod types, or were these higher taxa based on delayed recognition? Answering this question first for the copepod orders, it was seen that the genera upon which all 10 principal groups are based had been defined between 1776 and 1977, with 8 by 1891 and with 7 by 1865. The range of time between discovery of the genus and the recognition that it represented an entirely new major copepod division was 0 yr, for Siphonostomatoida, to 88 yr, for Mormonilloida. The average time from discovery of the genus to the definition of the order for which that genus is the type was 51 yr. That the earliest order, Cyclopoida, was defined in 1835 does not

Table 1.—Copepod classification to family, including type genera of families (modifications to Bowman & Abele (1982) indicated by *). The original date of a preoccupied and replaced genus name is indicated by PN.

*Subclass Copepoda Milne Edwards, 1830

Order Calanoida Sars, 1903

Acartiidae Sars, 1903

Acartia Dana, 1846

Aetideidae Giesbrecht, 1892

Aetideus Brady, 1883

Arietellidae Sars, 1902

Arietellus Giesbrecht, 1892

Augaptilidae Sars, 1905

Augaptilus Giesbrecht, 1889

Bathypontiidae Brodsky, 1950

Bathypontia Sars, 1905

*Boholiniidae Fosshagen & Iliffe, 1989

Boholina Fosshagen, 1989

Calanidae Dana, 1849

Calanus Leach, 1816

Calocalanidae Bernard, 1958

Calocalanus Giesbrecht, 1888

Candaciidae Giesbrecht, 1892

Candacia Dana, 1846

Centropagidae Giesbrecht, 1892

Centropages Krøver, 1849

Clausocalanidae Giesbrecht, 1892

Clausocalanus Giesbrecht, 1888

Diaixidae Sars, 1902

Diaixis Sars, 1902

Diaptomidae Baird, 1850

Diaptomus Westwood, 1836

Discoidae Gordejeva, 1975

Disco Grice & Hulsemann, 1965

Epacteriscidae Fosshagen, 1973

Epacteriscus Fosshagen, 1973

Eucalanidae Giesbrecht, 1892

Eucalanus Dana, 1852

Euchaetidae Giesbrecht, 1892

Euchaeta Philippi, 1843

Heterorhabdidae Sars, 1902

Heterorhabdus Giesbrecht, 1898 (PN 1863)

Lucicutiidae Sars, 1902

Lucicutia Giesbrecht, 1898 (PN 1863)

Mecynoceridae Andronov, 1973

Mecynocera I. C. Thompson, 1888

Megacalanidae Sewell, 1947

Megacalanus Wolfenden, 1904 Mesaiokeratidae Matthews, 1961

Mesaiokeras Matthews, 1961

Metridiidae Sars, 1902

Metridia Boeck, 1865

Paracalanidae Giesbrecht, 1892

Paracalanus Boeck, 1865

Parapontellidae Giesbrecht, 1892

Parapontella Brady, 1878

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830

Phaennidae Sars, 1902

Phaenna Claus, 1863

Phyllopodidae Brodsky, 1950

Phyllopus Brady, 1883

Pontellidae Dana, 1853

Pontella Dana, 1846 (PN 1828)

Pseudocyclopidae Giesbrecht, 1893

Pseudocyclops Brady, 1872

Pseudocyclopiidae Sars, 1902

Pseudocyclopia T. Scott, 1892

Pseudodiaptomidae Sars, 1902

Pseudodiaptomus Herrick, 1884

Ridgewayiidae M. S. Wilson, 1958

Ridgewayia I. C. Thompson & A. Scott, 1903

Ryocalanidae Andronov, 1974

Ryocalanus Tanaka, 1956

Scolecithricidae Giesbrecht, 1892

Scolecithrix Brady, 1883

Spinocalanidae Vervoort, 1951

Spinocalanus Giesbrecht, 1888

Stephidae Sars, 1902

Stephos T. Scott, 1892

Sulcanidae Nicholls, 1945

Sulcanus Nicholls, 1945

Temoridae Giesbrecht, 1892

Temora Baird, 1850

Tharybidae Sars, 1902

Tharybis Sars, 1902

Tortanidae Sars, 1902

Tortanus Giesbrecht, 1898 (PN 1883)

Order Harpacticoida Sars, 1903

Adenopleurellidae Huys, 1990

Adenopleurella Huys, 1990

Aegisthidae Giesbrecht, 1892

Aegisthus Giesbrecht, 1891

Ambunguipedidae Huys, 1990

Ambunguipes Huys, 1990

Ameiridae Monard, 1927

Ameira Boeck, 1865

Ancorabolidae Sars, 1909

Ancorabolus Norman, 1903

Balaenophilidae Sars, 1910

Balaenophilus P. O. Aurivillius, 1879

Cancrincolidae Fiers, 1990

Cancrincola C. B. Wilson, 1913

Canthocamptidae Sars, 1906

Canthocamptus Westwood, 1836

Canuellidae Lang, 1948

Canuella T. & A. Scott, 1893

Cerviniidae Sars, 1903

Cervinia Brady, 1878

Chappuisiidae Chappuis, 1940

Chappuisius Kiefer, 1938

Cletodidae T. Scott, 1904

Cletodes Brady, 1872

Table 1.—Continued.

Cristacoxidae Huys, 1990 Cristacoxa Huys, 1990 Cylindropsyllidae Sars, 1909

Cylindropsyllus Brady, 1880

Darcythompsoniidae Lang, 1936

Darcythompsonia T. Scott, 1906

Diosaccidae Sars, 1906

Diosaccus Boeck, 1872 Ectinosomatidae Sars, 1903

Ectinosoma Boeck, 1865

Hamondiidae Huvs, 1990

Hamondia Huys, 1990

Harpacticidae Dana, 1846

Harpacticus Milne Edwards, 1840

Laophontidae T. Scott, 1904 Laophonte Philippi, 1840

Latremidae Bozic, 1969

Latremus Bozic, 1969

Longipediidae Sars, 1903

Longipedia Claus, 1863

Louriniidae Monard, 1927

Lourinia C. B. Wilson, 1924 (PN 1866)

Metidae Sars, 1910

Metis Philippi, 1843

Miraciidae Dana, 1846

Miracia Dana, 1846

Neobradyidae Olofsson, 1917

Neobradya T. Scott, 1892

Paramesochridae Lang, 1948

Paramesochra T. Scott, 1892

Parastenheliidae Lang, 1936 Parastenhelia I. C. Thompson & A. Scott, 1903

Parastenocaridae Chappuis, 1933

Parastenocaris Kessler, 1913

Peltidiidae Sars, 1904

Peltidium Philippi, 1839

Phyllognathopodidae Gurney, 1932

Phyllognathopus Mrazek, 1893

Porcellidiidae Sars, 1904

Porcellidium Claus, 1860 (PN 1840)

Pseudopeltidiidae Poppe, 1891

Clytemnestra Dana, 1848

Tachidiidae Sars, 1909

Tachidius Lilljeborg, 1853

Tegastidae Sars, 1904

Tegastes Norman, 1903

Tetragonicepsidae Lang, 1944

Tetragoniceps Brady, 1880

Thalestridae Sars, 1905

Thalestris Claus, 1863

Tisbidae Stebbing, 1910

Tisbe Lilljeborg. 1853

Order Cyclopoida Burmeister, 1835

Archinotodelphyidae Lang, 1949

Archinotodelphys Lang, 1949

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830

Ascidicolidae Thorell, 1859

Ascidicola Thorell, 1859

Botryllophillidae Sars, 1921

Botryllophilus Hesse, 1864

Buproridae Thorell, 1859

Buprorus Thorell, 1859

Cyclopidae Dana, 1853

Cyclops Muller, 1776 Cyclopinidae Sars, 1913

Cyclopina Claus, 1863

Doropygidae Brady, 1878

Doropygus Thorell, 1859

Enterocolidae Sars, 1921

Enterocola van Beneden, 1860

*Enteropsidae C. W. S. Aurivillius, 1885 Enteropsis C. W. S. Aurivillius, 1885

*Lernaeidae C. B. Wilson, 1917

Lernaea Linnaeus, 1758

*Mantridae Leigh-Sharpe, 1934

Mantra Leigh-Sharpe, 1934

Notodelphyidae Dana, 1853

Notodelphys Allman, 1847

Oithonidae Dana, 1853

Oithona Baird, 1843

Ozmanidae Ho & Thatcher, 1989

Ozmana Ho & Thatcher, 1989

*Phyllodicolidae Delamare-Deboutteville & Laubier,

Phyllodicola Delamare-Deboutteville & Laubier, 1960

*Schizoproctidae C. W. S. Aurivillius, 1885

Schizoproctus C. W. S. Aurivillius, 1885

Speleoithonidae da Rocha & Iliffe, 1991 Speleoithona da Rocha & Iliffe, 1991

Order Poecilostomatoida Thorell, 1859

*Amazonicopeidae Thatcher, 1986 Amazonicopeus Thatcher, 1986

Anchimolgidae Humes & Boxshall, 1996

Anchimolgus Humes & Stock, 1972

Anomoclausiidae Gotto, 1964

Anomoclausia Gotto, 1964 Anomopsyllidae Sars, 1921

Anomopsyllus Sars, 1921

*Antheacheridae M. Sars, 1870 Antheacheres M. Sars, 1857

*Anthessiidae Humes, 1986

Anthessius Della Valle, 1880

*Bomolochidae Claus, 1875

Bomolochus von Nordmann, 1832

Catiniidae Bocquet & Stock, 1957

Catinia Bocquet & Stock, 1957

Chondracanthidae Milne Edwards, 1840

Chondracanthus Delaroche, 1811

Clausidiidae Embleton, 1901

Clausidium Kossmann, 1874

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830

Clausiidae Giesbrecht, 1895 Clausia Claparede, 1863

Corallovexiidae Stock, 1975

Corvcaeidae Dana, 1852

Corveaeus Dana, 1845

Cucumaricolidae Bouligand & Delamare-Deboutteville, 1959

Cucumaricola Peterson, 1958

Echiurophilidae Delamare-Deboutteville & Nunes-Ruivo, 1955

Echiurophilus Delamare-Deboutteville & Nunes-Ruivo, 1955

*Entobiidae Ho, 1984

Entobius Dogiel, 1908

*Erebonasteridae Humes, 1987 *Erebonaster* Humes, 1987

*Ergasilidae Burmeister, 1835 Ergasilus von Nordmann, 1832

Eunicicolidae Sars, 1918

Eunicicola Kurz, 1877

Gastrodelphyidae List, 1889

Gastrodelphys Graeffe, 1883 *Herpyllobiidae Hansen, 1892

Herpyllobius Steenstrup & Lutken, 1861

Intramolgidae Marchenkov & Boxshall, 1995
Intramolgus Marchenkov & Boxshall, 1995

Kelleriidae Humes & Boxshall, 1996

Kelleria Gurney, 1927

Lichomolgidae Kossmann, 1877 Lichomolgus Thorell, 1859

Macrochirontidae Humes & Boxshall, 1996

Macrochiron Brady, 1872

*Mesoglicolidae de Zulueta, 1911

Mesoglicola Quidor, 1906

Myicolidae Yamaguti, 1936

Myicola Wright, 1885

Mytilicolidae Bocquet & Stock, 1957

Mytilicola Steuer, 1902

Nereicolidae Claus, 1875

Nereicola Keferstein, 1863

Nucellicolidae Lamb, Boxshall, Mill, & Grahame, 1996

Nucellicola Lamb, Boxshall, Mill, & Grahame, 1996

Octopicolidae Humes & Boxshall, 1996

Octopicola Humes, 1957

Oncaeidae Giesbrecht, 1892

Oncaea Philippi, 1843

*Paralubbockiidae Boxshall & Huys, 1990 Paralubbockia Boxshall, 1977

Pharodidae Illg, 1948

Pharodes C. B. Wilson, 1935

*Philichthyidae Vogt, 1877

Philichthys Steenstrup, 1862

Table 1.—Continued.

*Subclass Copepoda Milne Edwards, 1830

Philoblennidae Izawa, 1976 Philoblenna Izawa, 1976

Pseudanthessiidae Humes & Stock, 1972 Pseudanthessius Claus, 1889

*Rhynchomolgidae Humes & Stock, 1972 Rhynchomolgus Humes & Ho, 1967

Sabelliphilidae Gurney, 1927 Sabelliphilus M. Sars, 1862

Sapphirinidae Thorell, 1859

Sapphirina J. V. Thompson, 1829

Serpulidicolidae Stock, 1979

Serpulidicola Southward, 1964

Shiinoidae Cressey, 1975

Shiinoa Kabata, 1968

*Spiophanicolidae Ho, 1984 Spiophanicola Ho, 1984

Splanchnotrophidae Norman & T. Scott, 1906 Splanchnotrophus Hancock & Norman, 1863

Synapticolidae Humes & Boxshall, 1996 Synapticola Voigt, 1892

Synaptiphilidae Bocquet & Stock, 1957

Synaptiphilus Canu & Cuenot, 1892 Taeniacanthidae C. B. Wilson, 1911

Taeniacanthus Sumpf, 1871 *Tegobomolochidae Avdeev, 1978

Tegobomolochus Izawa, 1976

Telsidae Ho, 1967 Telson Pearse, 1952

Thamnomolgidae Humes & Boxshall, 1996 Thamnomolgus Humes, 1969

Tuccidae Vervoort, 1962

Tucca Krøyer, 1837

Urocopiidae Humes & Stock, 1972

Urocopia Sars, 1917

Vahiniidae Humes, 1967

Vahinius Humes, 1967

*Vaigamidae Thatcher & Robertson, 1984 Vaigamus Thatcher & Robertson, 1984

Xarifiidae Humes, 1960 Xarifia Humes, 1960

Order Siphonostomatoida Thorell, 1859

Artotrogidae Brady, 1880

Artotrogus Boeck, 1859

Ascomyzontidae Thorell, 1859

Ascomyzon Thorell, 1859

Asterocheridae Giesbrecht, 1899 Asterocheres Boeck, 1859

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Brychiopontiidae Humes, 1974 Brychiopontius Humes, 1974

Caligidae Burmeister, 1835

Caligus Muller, 1785

*Calverocheridae Stock, 1968 Calverocheres C. B. Wilson, 1932 (PN 1902)

Cancerillidae Giesbrecht, 1897

Cancerilla Dalyell, 1851

Table 1.—Continued.

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*Subclass Copepoda Milne Edward	ls, 1830
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Catlaphilidae Tripathi, 1960 Catlaphila Tripathi, 1960

Cecropidae Dana, 1852 Cecrops Leach, 1816

Choniostomatidae Hansen, 1887 Choniostoma Hansen, 1887 Chordeumiidae Boxshall, 1988

Chordeumium Stephensen, 1918

Coralliomyzontidae Humes & Stock, 1991 Coralliomyzon Humes & Stock, 1991

*Dichelesthium Hermann, 1804

Dinopontiidae Murnane, 1967

Dinopontius Stock, 1960

Dirivultidae Humes & Dojiri, 1980 Dirivultus Humes & Dojiri, 1980

Dissonidae Yamaguti, 1963 Dissonus C. B. Wilson, 1906

Dyspontiidae Giesbrecht, 1895

Dyspontius Thorell, 1859

Ecbathyrion tidae Humes, 1987 Ecbathyrion Humes, 1987

Entomolepidae Brady, 1899

Entomolepis Brady, 1899

*Eudactylinidae C. B. Wilson, 1932 Eudactylina van Beneden, 1853

Euryphoridae C. B. Wilson, 1905 Euryphorus Milne Edwards, 1840

Hatschekiidae Kabata, 1979 Hatschekia Poche, 1902

Hyponeoidae Heegaard, 1962

Hyponeo Heegaard, 1962

Kroyeriidae Kabata, 1979 Kroyeria van Beneden, 1853

*Lamippidae Joliet, 1882 Lamippe Bruzelius, 1858

Lernaeoceridae Gurney, 1933

Lernaeocera de Blainville, 1822 *Lernaeopodidae Milne Edwards, 1840

Lernaeopoda de Blainville, 1822

Lernanthropidae Kabata, 1979

Lernanthropus de Blainville, 1822

Megapontiidae Heptner, 1968

Megapontius Hulsemann, 1965 Micropontiidae Gooding, 1957

Micropontidae Gooding, 1957

Micropontius Gooding, 1957

Myzopontiidae Sars, 1915

Myzopontius Giesbrecht, 1895

Nanaspididae Humes & Cressey, 1959

Nanaspis Humes & Cressey, 1959

Naobranchiidae Yamaguti, 1939 Naobranchia Hesse, 1863

Nicothoidae Dana, 1852

Nicothoe Audouin & Milne Edwards, 1826

*Subclass Copepoda Milne Edwards, 1830

Pandaridae Milne Edwards, 1840

Pandarus Leach, 1816

Pennellidae Burmeister, 1835

Pennella Oken, 1816

Pontoeciellidae Giesbrecht, 1895

Pontoeciella Giesbrecht, 1895

Pseudocycnidae C. B. Wilson, 1922

Pseudocycnus Heller, 1865 Rataniidae Giesbrecht, 1897

Ratania Giesbrecht, 1892

Saccopsidae Lutzen, 1964

Saccopsis Levinsen, 1878

*Sphyriidae C. B. Wilson, 1919

Sphyrion Cuvier, 1830

Spongiocnizontidae Stock & Kleeton, 1964 Spongiocnizon Stock & Kleeton, 1964

Stellicomitidae Humes & Cressey, 1958

Stellicomes Humes & Cressey, 1958

Stellicomes Humes & Cressey, 1958

Tanypleuridae Kabata, 1969

Tanypleurus Steenstrup & Lutken, 1861

*Trebiidae C. B. Wilson, 1905 Trebius Krøyer, 1838

Ventriculinidae Leigh-Sharpe, 1934 Ventriculina Bassett-Smith, 1903

Xenocoelomatidae Bresciani & Lutzen, 1966 Xenocoeloma Caullery & Mesnil, 1915

Order Monstrilloida Sars, 1903

*Monstrillidae Dana, 1849 Monstrilla Dana, 1849

*Order Misophrioida Gurney, 1927

Misophriidae Brady, 1878 Misophria Boeck, 1865

Order Mormonilloida Boxshall, 1979

Mormonillidae Giesbrecht, 1892 Mormonilla Giesbrecht, 1891

*Order Platycopioida Fosshagen, 1985

Platycopiidae Sars, 1911 Platycopia Sars, 1911

*Order Gelyelloida Huys, 1988

Gelyellidae Rouch & Lescher-Moutoue, 1977 Gelyella Rouch & Lescher-Moutoue, 1977

Order uncertain

Chitonophilidae Avdeev & Sirenko, 1991 Chitonophilus Avdeev & Sirenko, 1991

Sponginticolidae Topsent, 1928

Sponginticola Topsent, 1928 Staurosomatidae de Zulueta, 1911

Staurosoma Will, 1844

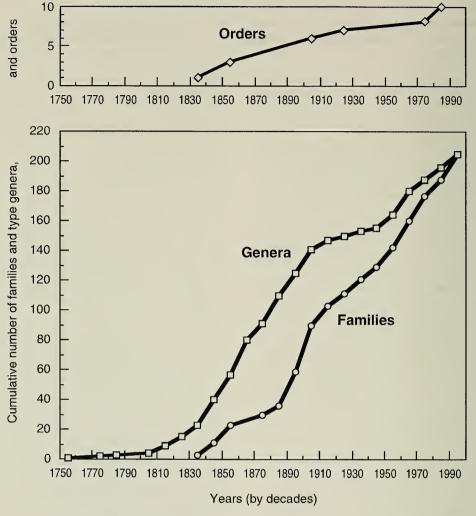


Fig. 1. Cumulative number of defined families, type genera, and orders of copepods, by decade, from 1750 to 1996.

mean that there were no other order-level taxa at that time, but that the other analogous groups have fallen out of favor in the meantime.

This prompted a similar approach toward the families: were they indicative of newly discovered family-level Copepoda, or were they mostly the result of deliberative comparison of accumulating genus descriptions? This was not so easily answered; a foray into the literature spread across the whole of Copepoda to determine the type-genus (and date) for each family was not trivial. This is

also a dynamic process, and undoubtedly alterations and additions are now occurring. In fact, seven families were described in 1996 after the first draft was completed. As with Bowman & Abele, I do not provide references for the indicated authors; this would be beyond the intention of the survey. Some type genera are dated from the time a new name was proposed to replace a preoccupied name; in these cases I have used the older date for the calculations, since the discovery was based on the earlier date; these extended dates are indicated in Table 1.

A third relationship (Fig. 1) shows the time-dependency of the descriptions of what became type-genera for families. The indication, when comparing the family and type-genus curves, is that copepodologists are in general a conservative company. Over the preceding 160 yr, 54 families (26%) were proposed at the time that the type genus was described. (These "instant" families arose between 1846 and 1996, with the median year of 1963; that is, the phenomenon is skewed to recent years, as one might expect given the accumulated background of defined families.) Another way to look at this is that most of the fundamental (family) copepod types were discovered long before they were recognized as such. Overall, the average delay time was 31 yr, with a range of 0 to 159 yr. Excluding the families that were defined at the time the type genus was described, the average delay time for family definition was 42 yr. If the type species, rather than the type genus, is considered, the dates would be set back even farther in some cases, although probably not significantly so.

Note that 10 genera would define the present 10 orders, just as the 205 type genera basically define the 205 families. All the many other genera are superfluous, except, of course, that they define the *limits* of higher taxa already defined in their essentials.

Can we use the curves to make predictions? The type-genus curve cannot be predictive, mainly because it does not exist until families are defined; a predictive genus curve would have to include the many more genera besides type genera. The genus curve should not be compared within decades to the family curve; the only comparison should be horizontal, reflecting the time lags. Since families must await the discovery of their type genera, there will always, in general, be a lag time. Recently discovered genera that become type genera force the two curves to converge, since there is obviously not much time available for a newly discovered genus to have become the type of a new family. Future association of the two curves depends on whether families are made from recently described genera (the curves will remain together) or from older genera (the curves will again separate). The availability of large numbers of well-defined families potentially makes it easier to discern new families with the discovery of new genera or with reconsideration of older genera. Clearly, a trend to be avoided would be the creation of a new family from each genus, thereby defeating the notion of a classification hierarchy.

There is no trend suggesting that families might not be defined at the previous rate, or that we are running out of new families. Of course, as new habitats are explored, such as caves and deep-ocean thermal vents, new genera representing new families would be expected. Given the present dynamics of copepod taxonomy, predictions may require a few more decades of observation.

Even without the discovery of absolutely new types, taxa above genera will be added as more details, especially of developmental biology, are added to the framework in place and more comparisons are made. Copepod taxonomy has long been vexed by many imperfectly described species, and a re-working of these will add some surprises. Also, there are some copepod families that cannot now be placed into the defined orders; there are also many genera that are not yet assigned to families. These may be raw material for additional higher taxa, or the discovery of intermediate species may link them to established groups. There is a wealth of material to contemplate, with future intensive rearranging. However, eventually there will be no more orders and no more families to discover.

For those who are depressed by this prospect, and fear coming idleness, there is an infinitude of related research to be done. I offer the insight of Herman Melville (1851): "Dissect him how I may, then, I but

go skin deep; I know him not, and never will."—Moby Dick, Chapter 86.

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